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Erketu ellisoni, a Long-Necked Sauropod from Bor Guvé (Dornogov Aimag, Mongolia)

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ABSTRACT

The first specimen of the new sauropod *Erketu ellisoni*, from the Lower Cretaceous of the eastern Gobi of Dornogov, Mongolia, is described here. The specimen comprises a well-preserved articulated anterior cervical series, an articulated lower hindlimb, and a sternal plate. This sauropod displays a unique combination of features including low, bifid neural spines, elongate cervical centra, and crescent-shaped sternal plates. Computed tomography imaging reveals the vertebrae were extensively invaded with pneumatic camellae. The holotype individual of *Erketu* was of modest mass relative to other neosauropods, but had an extremely elongate neck. Phylogenetic analysis indicates *Erketu* is a member of the Somphospondyli and may belong to a more exclusive clade therein.

INTRODUCTION

The 2002 American Museum of Natural History–Mongolian Academy of Sciences field expedition discovered a new locality, Bor Guvé, in Dornogov Aimag, Mongolia (fig. 1). Several sauropod cervical vertebrae were found eroding out of the surface at this locality, and excavation revealed the rest of the anterior cervical series preserved in articulation directly in front of these elements. Additional postcranial elements were uncovered as the cervicals were being collected. Despite exhaustive efforts, no skull was found in the vicinity of the atlas.

The first sauropod remains described from Mongolia were two teeth collected by the American Museum of Natural History Central Asiatic Expeditions at the Lower Cretaceous Ööshiin Nuur locality (Osborn, 1924). These teeth were assigned to *Asiatosaurus mongoliensis*, a name now considered a nomen dubium (McIntosh, 1990). The Central Asiatic Expeditions also collected a basioccipital, three cervical vertebrae, and several teeth of the poorly known sauropod *Monoglosaurus haplodon* from the Lower Cretaceous Hu Khung Ulan locality (Gilmore, 1933). Several important sauropod specimens have since been recovered from Upper Cretaceous deposits, including the nearly complete postcranial skeleton of *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977) and skull of *Nemegtosaurus*, collected by the

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Fig. 1. Map of Mongolia showing the location of Bor Guvé.

Polish–Mongolian expeditions (Nowinski, 1971), and the skull of *Quesitosaurus*, collected by the Soviet–Mongolian expeditions (Kurzanov and Bannikov, 1983). With the exception of these discoveries, sauropod material from Mongolia has been scarce and fragmentary. The discovery of *Erketu* provides an important addition to Mongolian sauropod diversity.

The deposits at Bor Guvé appear to represent a floodplain environment. Interbedded grey siltsones and channel sandstones dominate. Lag deposits have yielded turtle remains and dinosaur teeth, and sauropod and theropod remains have been recovered from the siltsones. Among the theropod material uncovered at this site are elements from a maniraptoran slightly larger than *Deinonychus* and an *Allosaurus*-sized predatory theropod. Fossil fruits (fig. 2) from a probable angiosperm plant of unknown affinity are locally abundant at the locality. These fruits bear a superficial resemblance to extant *Abelmoschus esculentus* (okra). The fruits are not, to our knowledge, assignable to any known taxon, and are currently being described (Koppelhus, in prep.). Indistinguishable fossil fruits have been collected from the stratigraphically lower Khara Khuutal beds, which crop out to the east.

In describing the morphology of the vertebrae, we use the terminology and abbreviations for vertebral lamina proposed by Wilson (1999) and the terminology for pneumatic features proposed by Wedel et al. (2000). Computed tomography (CT) scans were performed at the Stony Brook University Hospital Radiology Department, using a GE Light Speed 16 scanner.

ABBREVIATIONS

INSTITUTIONAL: **AMNH**, American Museum of Natural History, New York, New York, USA; **CM**, Carnagie Museum of Natural History, Pittsburgh, Pennsylvania, USA; **CCG**, Chengdu College of Geology, Sichuan, China; **HM**, Humbolt Museum, Berlin, Germany; **IGM**, Geological Institute of the Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; **OMNH**, Oklahoma Museum of Natural History, Norman,

Fig. 2. Fossil fruits from Bor Guvé. Scale bar = 1 cm.

Oklahoma, USA; **PMU**, Paleontological Museum, Uppsala, Sweden; **ZDM**, Zigong Dinosaur Museum, Zigong, China.

ANATOMICAL: **ap**, accessory anterior process of prezygodiapophyseal lamina; **ax**, axis; **cml**, camella; **cr**, cervical rib; **ic**, intercentrum of atlas; **mtp**, metapophysis; **np**, neurapophysis of atlas; **pcdl**, posterior centrodiapophyseal lamina; **pcpl**, posterior centroparapophyseal lamina; **pdol**, postzygodiapophyseal lamina; **pfm**, pneumatic foramen; **pfs**, pneumatic fossa; **prdl**, prezygodiapophyseal lamina; **prz**, prezygapophysis; **tb,** tubercle; **td**, torus dorsalis, **tp**, transverse process.

SYSTEMATIC PALEONTOLOGY

SAUROPODA MARSH, 1878

NEOSAUROPODA BONAPARTE, 1986

MACRONARIA WILSON AND SERENO, 1998

TITANOSAURIFORMES SALGADO, CORIA, AND CALVO, 1997

SOMPHOSPONDYLI WILSON AND SERENO, 1998

Erketu ellisoni new taxon

HOLOTYPE: IGM 100/1803: articulated cervical series including complete first through fifth cervical vertebrae, partial sixth cervical vertebra, right sternal plate, articulated right tibia, fibula, astragalus, and calcaneum.

ETYMOLOGY: *Erketu*: In Mongolian shamanistic tradition, there are 99 Tengri (deities). Erketü Tengri is the Mighty Tengri, a creator-god who called Yesügei, the father of Chingis Khan, into being. *ellisoni*: In honor of Mick Ellison, for his contributions to ongoing AMNH dinosaur research.

DIAGNOSIS: Referable to Titanosauriformes based on elongate cervical vertebrae with camellae and referable within Titanosauriformes to Somphospondyli based on reduced neural arch lamination. Differentiated from all other Titanosauriformes in which cervical vertebrae are known by combination of extremely elongated (EI indices of anterior cervicals exceeding 5.0) cervical centra and bifurcate anterior cervical neural spines.

TYPE LOCALITY AND HORIZON: Bor Guvé: late Early Cretaceous. Stratigraphically, the beds at this locality lie below the Tsaagan Tsonch beds (a unit that contains *Iguanodon orientalis*) and above the Khara Khuutul beds, both believed to be of late Early Cretaceous age (Shuvalov, 2000). The lack of materials suitable for radiometric dating leaves the exact age of this locality uncertain.

DESCRIPTION

AXIAL SKELETON

The atlas is complete and articulated with the axis (fig. 3). The intercentrum is crescentic in anterior view, though deformation has compressed the dorsal apices inward, causing it to appear more circular. In lateral view, the intercentrum is subrectangular. A roughened articular surface is present near the posteroventral corner of the lateral face. The wing-like neurapophyses embrace the neural spine of the axis. The fusion of the neurapophyses to the intercentrum and closure of all other neurocentral sutures indicates IGM 100/1803 represents an adult individual.

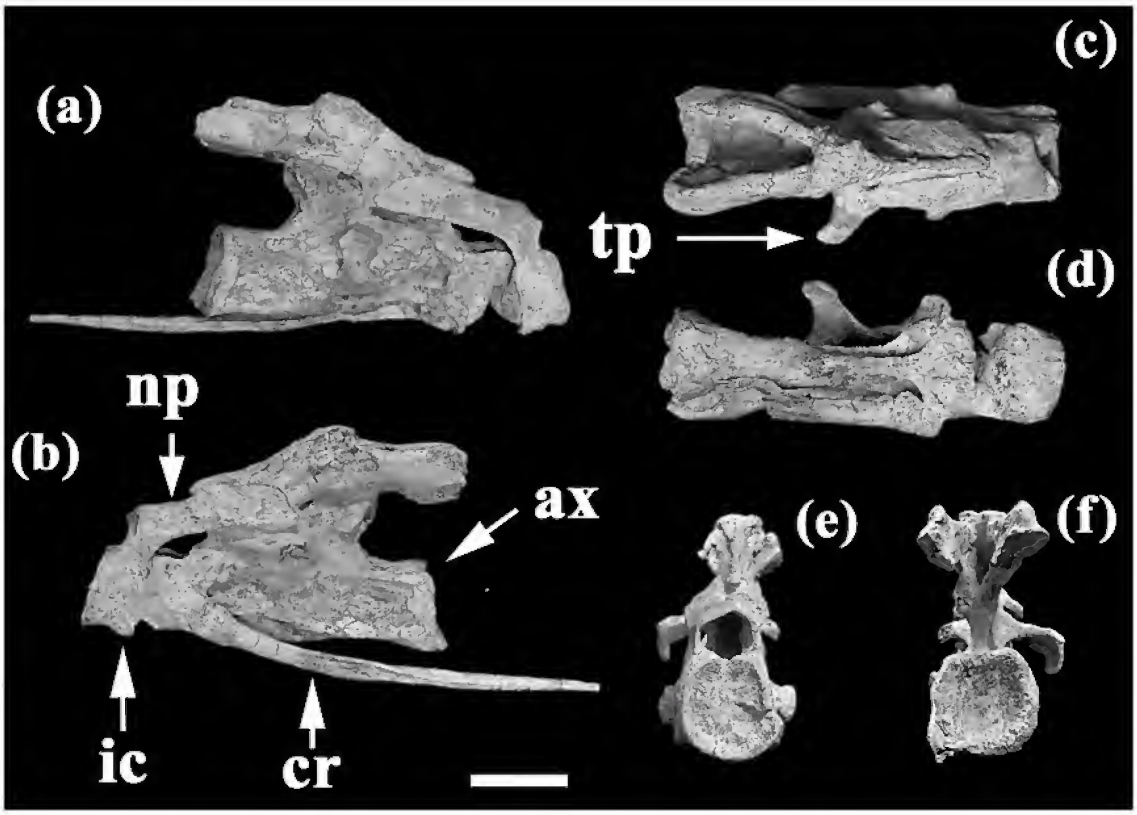

Fig. 3. Atlas and axis of IGM 100/1803 in (**a**) right lateral, (**b**) left lateral, (**c**) dorsal, (**d**) ventral, (**e**) anterior, and (**f**) posterior view. Note that the cervical rib has been detached in (**c**)–(**f**). For abbreviations, see text. Scale bar for (**a**), (**b**), (**c**), and (**d**) = 5 cm.

The axis is opisthocoelous with well-developed pneumatic fossae. The anterior half of the axial centrum develops a strong ventral keel. The cotyle is subcircular, with nearly equal height and width. The short transverse process has a ventrally directed distal flange. The anteriorly displaced parapophyses bear single-headed ribs that extend significantly beyond the posterior border of the axial centrum, though the total length is uncertain due to breakage. The axial neural spine barely projects dorsal to the level of the postzygapophyses. The low axial neural spine of *Erketu* is similar to that of the unnamed titanosaur from Peiropolis, Brazil, referred to as the "Series A" taxon (Powell, 2003) and the eusauropod *Mamenchisaurus sinocandorum* (Russell and Zheng, 1993; notably, the axial neural projects well dorsal to the postzygapophyses in the supposedly cogeneric *Mamenchisaurus houchuanensis*; Young and Zhou, 1972). Most titanosauriforms, including *Brachiosaurus* (Janesch, 1950: fig. 14), *Euhelopus* (Wiman, 1929: pl. 3, fig. 3), and *Saltasaurus* (Powell, 1992) have more dorsally projected axial neural spines.

The third (fig. 4) and succeeding cervical vertebrae have opisthocoelous centra with well-developed pneumatic fossae and variably developed laminae. The most striking feature of the cervical vertebrae is their elongation. The elongation index (EI, sensu Wedel et al., 2000: centrum length/cotyle height) exceeds those of all other sauropods for which comparable data are available (table 1). It should be noted that because the cotyle is taller than wide in *Erketu*, calculating EI as centrum length/cotyle width (sensu Upchurch, 1998) would increase the values for this taxon both absolutely and relative to most other sauropods. *Sauroposeidon proteles* (Wedel et al., 2000) and *Omeisaurus junghsiensis*

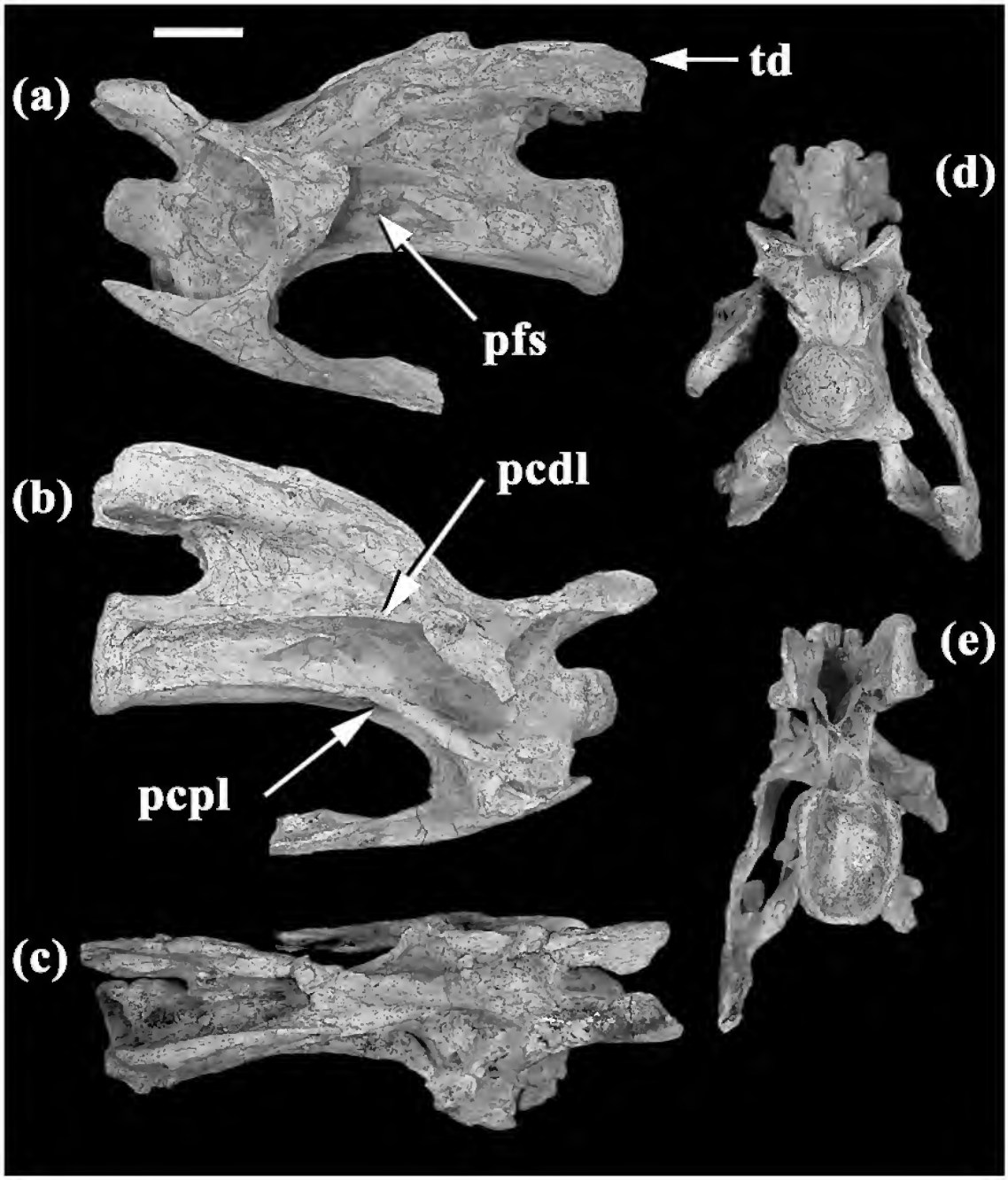

Fig. 4. Cervical 3 of IGM 100/1803 in (**a**) left lateral, (**b**) right lateral, (**c**) dorsal, (**d**) anterior, and (**e**) posterior view. For abbreviations, see text. Scale bar for (**a**), (**b**), and (**c**) = 5 cm.

(Young, 1939) also possess tremendously elongate vertebrae. However, only mid-cervicals are preserved for *S. proteles*, and in *O. junghsiensis* the preserved cervicals have suffered distortion of the cotyles and are of uncertain position, precluding direct comparison with *Erketu*.

As in *Euhelopus* and the primitive Asian eusauropods *Shunosaurus, Omeisaurus*, and *Mamenchisaurus*, the postaxial centra are

TABLE 1
Elongation Indices and Centrum Lengths from Various Sauropods
Values for *Erketu* are from this study, values for *Mamenchisaurus* are from Young and Zhou (1972), values for *Omeisaurus tianfuensis* are from He et al. (1988), and all other values are from Wedel et al. (2000). For *Erketu ellisoni*, C5 is dorsoventrally compressed, causing an artificially high EI value of 8.5. If cotyle width is used intead of height, a value of 5.8 is calculated; the true value would be slightly greater.

	Vertebra						
	C2	C3	C4	C5	C6	C7	C8
Centrum length (mm)							
Apatosaurus lousisae (CM 3018)	190	280	370	—	440	—	485
Brachiosaurus brancai (HM SII)	—	420	663	810	900	930	973
Camarasaurus supremus (AMNH 5761)	235	265	310	395	—	350	605
Diplodocus carnegii (CM 84)	163	243	289	372	442	485	512
***Erketu ellisoni* (IGM 100/1803)**	**160**	**268**	**387**	**489**	—	—	—
Euhelopus zdanskyi (PMU.R233)	94	130	222	234	238	260	262
Mamenchisaurus hochuanensis (CCG V 20401)	160	215	320	415	480	580	590
Omeisaurus tianfuensis (ZDM T5701)	170	241	368	495	595	670	673
Sauroposeidon proteles (OMNH 53062)	—	—	—	—	1220	1230	1250
Elongation index							
Apatosaurus lousisae (CM 3018)	2.2	3.0	3.3	—	3.2	—	2.9
Brachiosaurus brancai (HM SII)	—	3.5	4.3	5.4	5.0	4.4	4.0
Camarasaurus supremus (AMNH 5761)	1.9	2.5	2.3	2.3	—	3.1	3.5
Diplodocus carnegii (CM 84)	3.1	4.1	3.3	4.7	4.7	4.9	4.3
***Erketu ellisoni* (IGM 100/1803)**	**3.4**	**4.5**	**5.5**	**X**	—	—	—
Euhelopus zdanskyi (PMU.R233)	2.5	2.7	5.4	3.6	3.2	3.2	2.8
Mamenchisaurus hochuanensis (CCG V 20401)	2.0	2.5	2.6	2.8	2.9	2.9	2.7
Omeisaurus tianfuensis (ZDM T5701)	2.7	3.0	3.8	4.9	3.6	X	X
Sauroposeidon proteles (OMNH 53062)	—	—	—	—	6.1	5.6	4.6

significantly higher than wide at the cotyle (centrum six is wider than high due to dorsoventral deformation). The opposite condition is developed in the basal titanosaur *Phuwiangosaurus*, which has transversely expanded cervical vertebral centra (Martin et al., 1994). The lateral surface of each cervical centra in *Erketu* is marked by a large pneumatic fossa that reduces the centum to a thin median septum. The posterior centrodiapophyseal and posterior centroparapophyseal lamina are strongly developed along the area of the pneumatic fossa, but are weak near the posterior border of the centrum. A weakly developed lamina divides the large lateral pneumatic fossa from a smaller anterior pneumatic fossa in the anterior cervical vertebrae. However, this lamina is better developed in the sixth cervical vertebra, indicative of an expected increase in complexity of the fossae moving posterior in the vertebral column. The anterior pneumatic fossa extends ventrally onto the dorsal surface of the parapophyses on the third and fourth cervicals, where the parapophyses are preserved. Additional excavations are present on the centra and neural spines. The distribution of these minor excavations, of pneumatic foramina in the pneumatic fossa, and of similar features elsewhere on the vertebrae is highly variable and may even differ between the two sides of an individual vertebra. The posterior

centroparapophyseal laminae make the ventral surface of the anterior half of the centrum concave. Posteriorly, the ventral surface is slightly convex.

The neural arches of cervical vertebrae 3–5 are characterized by low, gently curving profiles. The prezygapophyses extend anterior of the condyle as in most sauropods. The prezygodiapophyseal lamina is unremarkable in cervical three. In the succeeding cervicals, however, it is hypertrophied and extends far anterior of the articular facet as a thin plate, oriented perpendicular to the articular plane (fig. 5). The primitive Saharan eusauropod *Jobaria* also possesses a similar morphology (Sereno et al., 1999: "accessory anterior process"). The postzygapophyses extend only slightly beyond the posterior border of the centrum. The postzygodiapophyseal lamina is poorly developed and fades from a sharp lamina to a low, rounded ridge a short distance posterior to the diapophysis. The pronounced torus dosalis extends posterior to the postzygapophyseal articular facet in cervicals four and five, though not in cervical three. The intrapostzygapophyseal lamina connect to the dorsal surface of the neural canal via a vertical strut. The neural arch laminae are reduced, but not to the degree seen in *Malawisaurus*. In lateral view, the cervical neural arches of *Erketu* resemble those of the "Series A" titanosaur and *Malawisaurus* more closely than the higher and more steeply angled neural arches of *Euhelopus* (Wiman, 1929: pl. 3, fig. 3) and *Brachiosaurus* (Janesch, 1950: figs. 17, 20, 23).

The neural spines of the fourth and succeeding cervicals are bifurcated. The metapophyses are very low and are thickened and rugose at their highest point. A small tubercle projects from each metapophysis at the anterior edge of the inflated portion (fig. 6). There is no median tubercle between the split neural spines, though this does not rule out the presence of this feature farther posterior in the cervical series. As mentioned above, pneumatic features of the neural spine are highly variable. Cervical four possesses a large, well-defined ovoid excavation that is subdivided by a bony strut on the left metapophysis, but no counterpart feature on the right.

The delicately tapering, double-headed ribs are completely fused to the diapophyses and parapophyses. An anterior projection of the rib extends to the anterior limit of the centrum. The main body of the most complete rib extends posteriorly to overlap at least one succeeding centrum, but it is incomplete at the posterior end and may have been significantly longer.

Computed tomography imaging reveals details of the internal structure of the fourth cervical vertebra (fig. 4). The centrum is reduced to a median plate by the pneumatic fossa at its midpoint. Anterior, posterior, and dorsal to the pneumatic fossa, the centrum is filled with pneumatic chambers. The small size, lack of regular branching pattern, and thinness of the septae dividing these chambers identify them as camellae. The presence of camellae extends into the diapophyses and parapophyses. The camellate structure of the latter is particularly highly developed. The internal structure of the cotyle and zygapophyses is unclear, possibly as an artifact of scanning resolution, though it appears the zygapophyses are at least somewhat pneumatized. A large foramen above the diapophysis of the fourth vertebrae appears to communicate with the neural canal (see fig. 7d).

A few camellae are exposed on the surface on the dorsal side of the condylar neck of the fifth cervical (fig. 8). The bone at the neck of the condyle is very thin, as seen in the CT imagery. In several places, the outer layer of bone has collapsed or been worn away, exposing camellae infilled with matrix. As exposed on the surface, the camellae are irregularly shaped, giving the bone surrounding them a honeycomb-like appearance. The exposed septae are approximately 1 mm thick. Larger camallae with thin septae are also exposed on the lateral surface of the damaged sixth vertebral centra.

Appendicular Skeleton

The sternal plate (fig. 9) exhibits a strongly concave lateral border, a feature seen in Titanosauria as well as in the rebbachisaurid *Limayosaurus tessonei* (Calvo and Salgado, 1995). The internal surface is concave posteriorly and nearly flat anteriorly. The external surface is gently convex posteriorly and nearly

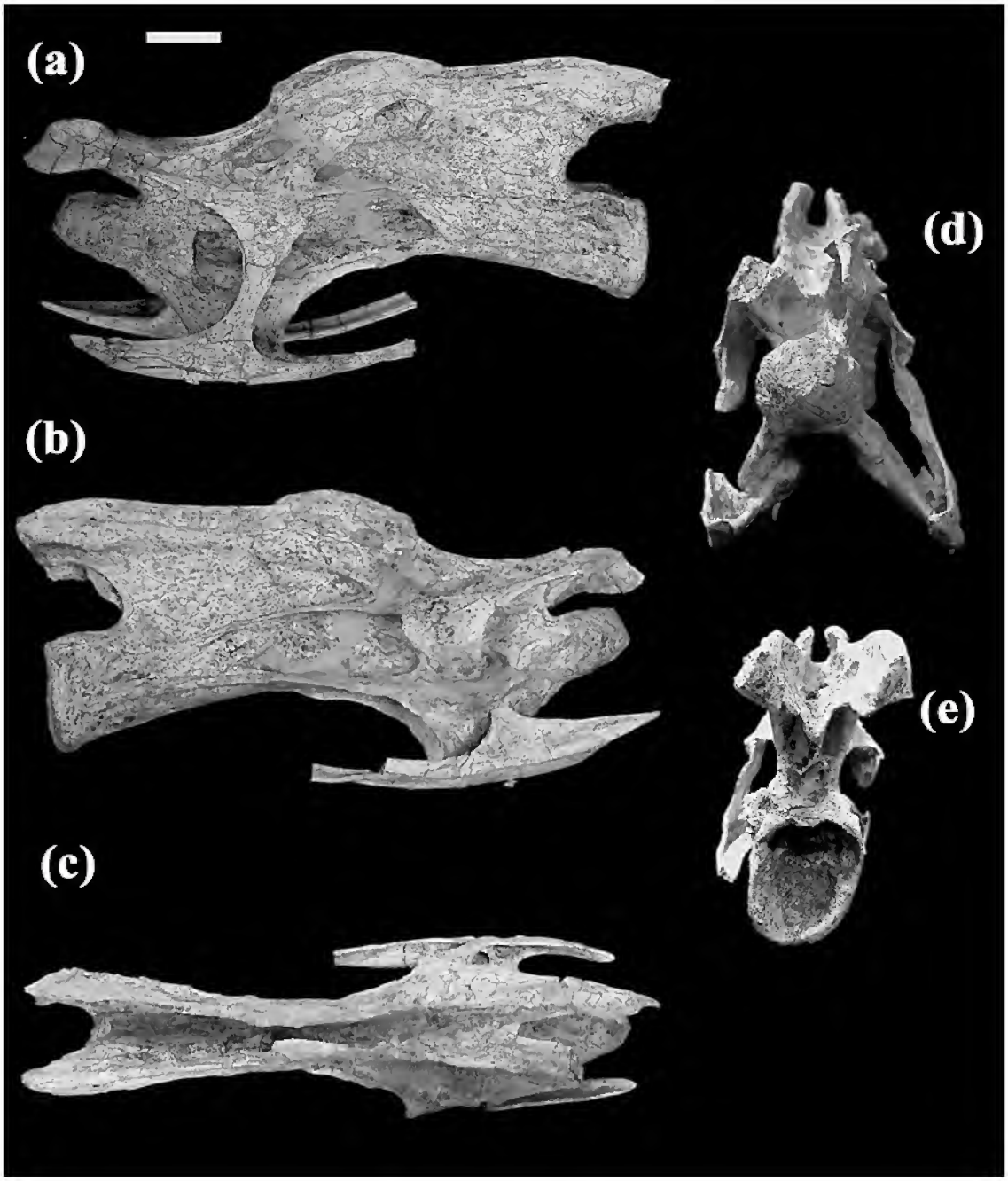

Fig. 5. Cervical 4 of IGM 100/1803 in (**a**) left lateral, (**b**) right lateral, (**c**) dorsal, (**d**) anterior, and (**e**) posterior view. For abbreviations, see text. Scale bar for (**a**), (**b**), and (**c**) = 5 cm.

flat anteriorly. The sternal plate is greatly thickened at the anterolateral corner, but lacks the anteroventral ridge developed in some titanosaurs (Sanz et al., 1999).

The right tibia, fibula, and astragalus (fig. 10) are preserved in articulation with only slight displacement. The hindlimb elements bear a strong overall resemblance to

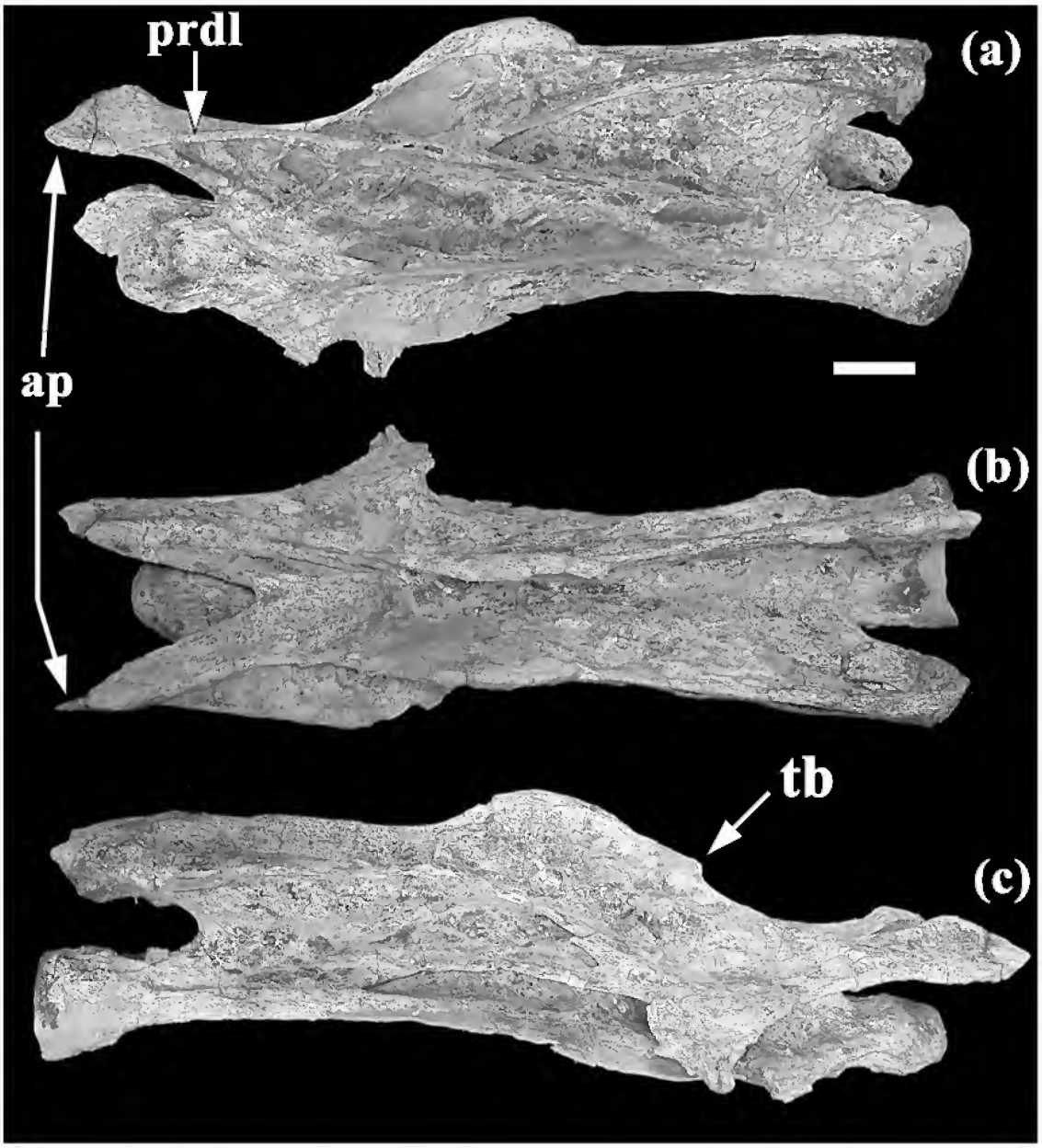

Fig. 6. Cervical 5 of IGM 100/1803 in (**a**) left lateral, (**b**) dorsal, and (**c**) right lateral view. This vertebra has been deformed so that the centrum appears artificially dorsoventrally flattened and the right diapophysis is visible ventrally in view **a**. For abbreviations, see text. Scale bar = 5 cm.

those of *Gobititan shenzhouensis*. The proximal face of the tibia is subcircular. The well-developed cnemial crest projects laterally, embracing the proximal end of the fibula. The greatest breadth at midshaft is in the anterolateral-posteromedial dimension, but at the distal end the transverse breath is greatest. The anterior and distal expansion of the tibia does not reach the degree seen in *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977).

The fibula extends distal to the tibia. The fibula is broken near the distal end of the lateral trochanter, and the sigmoid appearance of the shaft is slightly exaggerated by this

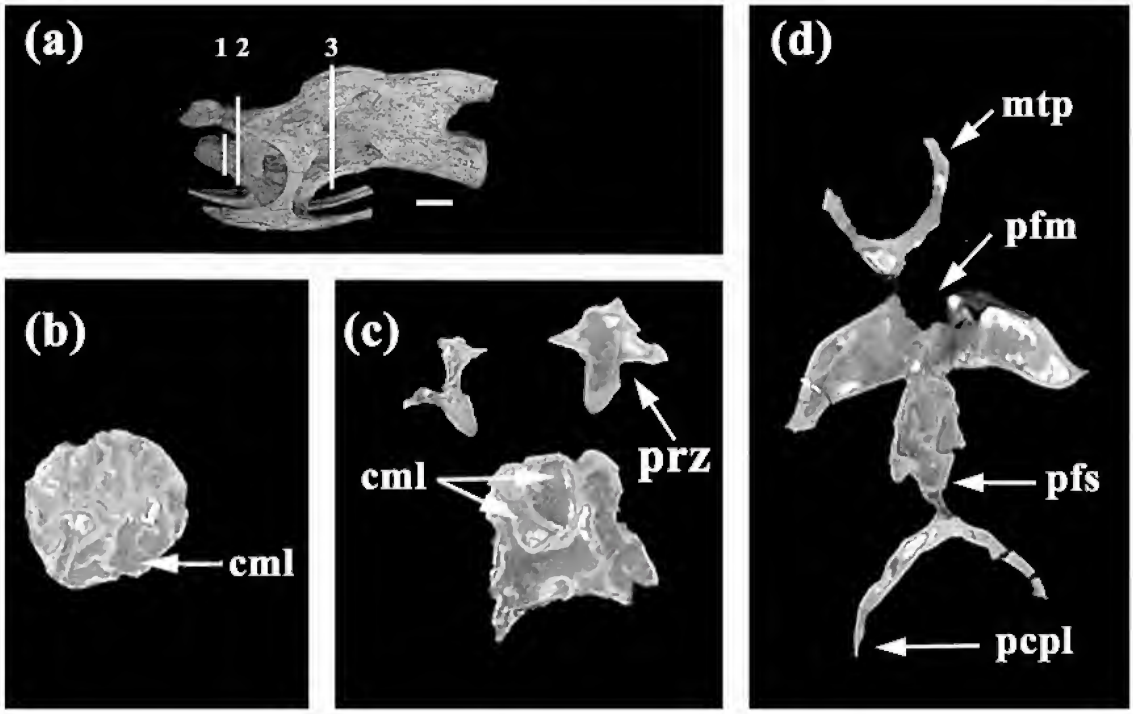

Fig. 7. Computed tomography images of cervical 4. (**a**) Lateral view of cervical 5 showing plane of coronal sections. Scale bar = 5 cm. (**b**) Section through position 1. (**c**) Section through position 2. (**d**) Section through position 3. For abbreviations, see text.

damage. The anterior and lateral trochanters arise approximately one-third of the bone's length from the proximal end on the anterolateral surface of the shaft, as in *Opisthocoelocaudia*. The trochanters are placed more distally in *Gobititan* (You et al., 2003). The anterior trochanter is short, whereas the lateral trochanter extends past the midpoint of the shaft and has a slight posterodistal slant. The anteromedial edge of the shaft

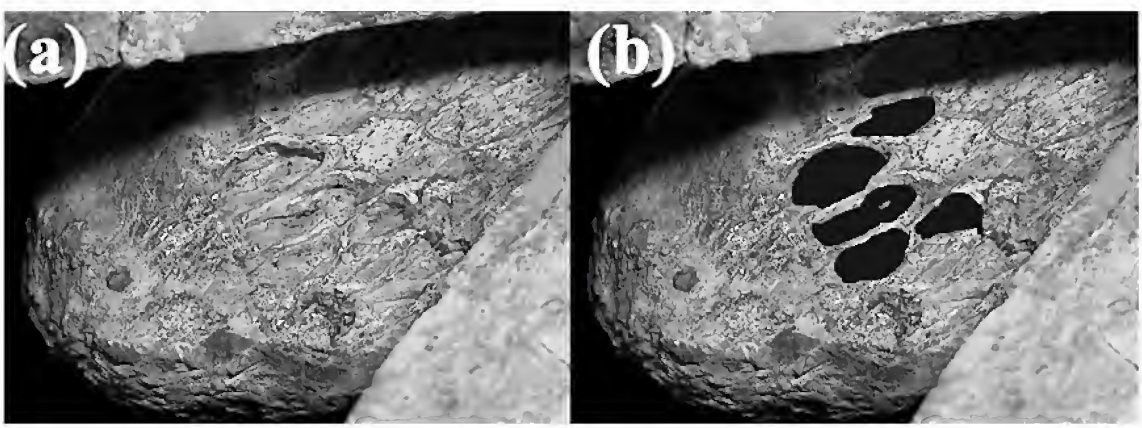

Fig. 8. Dorsal view of the condyle of cervical 5. View **(a)** is unmodified; in view **(b)** the exposed camellae are highlighted in dark gray.

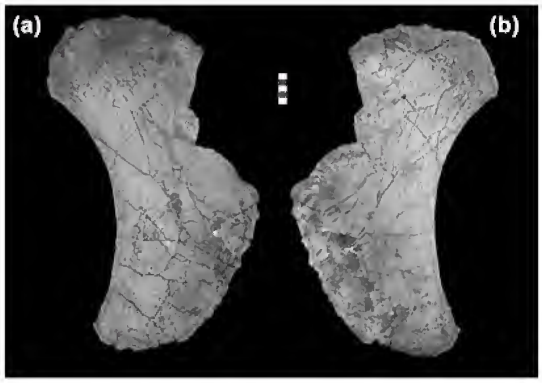

Fig. 9. Right sternal plate of IGM 100/1803 in (**a**) external and (**b**) visceral views. Scale bar = 5 cm.

develops into a sharp ridge near the distal end. The condyle is modestly expanded and has a slightly convex distal surface.

The morphology of the astragalus is difficult to observe because of its tight articulation with the tibia. In anterior view it exhibits the typical wedge shape of neosauropods (Wilson and Sereno, 1998). It fails to cap the entire distal end of the tibia, not reaching the medial border. An ossified calcaneum is present. It is a small, globular bone with a highly rugose surface texture and a flattened dorsal face. Although it remains debatable whether an ossified calcaneum was present in the Diplodocidae (see Bonnan, 2000), this element

Fig. 10. Right tibia, fibula, astragalus, and calcaneum of IGM 100/1803 in (**a**) anterior and (**b**) posterior views. Scale bar = 10 cm.

is known to be present in most sauropods, including *Euhelopus* and *Gobititan*. The lack of a calcaneum in the articulated hindlimb of the holotype of *Opisthocoelocaudia* is considered evidence of true absence (Borsuk-Bialynicka, 1977) in that taxon.

PHYLOGENETIC ANALYSIS

A phylogenetic analysis was conducted utilizing a matrix of 234 characters and 29 sauropod and outgroup taxa from an analysis by Wilson (2002) with the addition of *Erketu*. A single change was made to the original matrix, changing the coding for *Camarasaurus* for character 90 from 0 to 1. This change reflects the observation of Tshuihiji (2004) that a median tubercle is present between the posterior cervical neural spines in *Camarasaurus*. A branch and bound search conducted in PAUP*4.0b10 yielded six most parsimonious trees of 434 steps in which *Erketu* occupied one of two positions: the sister taxon of *Euhelopus* or the sister taxon of Titanosauria. The strict consensus of the six most parsimonious trees is presented in figure 11.

Erketu possesses two characters synapomorphic of Titanosauriformes in this analysis: presence of presacral camellae and elongate cervical centra. *Erketu* possesses one character of the more exclusive Somphospondyli: reduced cervical neural arch lamination. In the subset of trees supporting an *Erketu* + Titanosauria grouping, one character optimizes as an unambiguous synapomorphy of that clade: distally expanded tibia. A second character is ambiguously synapomorphic for this clade: crescent-shaped sternal plates (unknown in *Euhelopus*). In the subset of trees supporting a *Erketu* + *Euhelopus* grouping, one unambiguous synapomorphy supports that clade: cervical centra higher than wide.

Because many important characters are scored unknown for *Erketu*, and also because taxon sampling of the Titanosauria is incomplete, the phylogenetic position presented in figure 11 should be regarded as preliminary. As discussed below, we believe the association of additional postcranial and dental material with *Erketu* may lead to a revised placement within the Titanosauria.

DISCUSSION

The size of the preserved hindlimb elements suggests that *Erketu*, despite its great length, was of modest mass. The third, fourth, and fifth cervical vertebrae of *Erketu* are more elongate relative to the tibia than are the cervical vertebrae of the long-necked sauropods *Diplodocus carnegii*, *Omeisaurus tianfuensis, Mamenchisaurus hochuanensis*, and *Euhelopus zdanskyi*. Whether this indicates a proportionally longer neck relative to trunk height cannot be decided, as the forelimb, femur, and pes length and total cervical vertebral count of *Erketu* are not known.

Various sauropod taxa achieve elongation of the neck by increasing the length of the cervical vertebrae, the number of cervical vertebrae, or both. The long-necked titanosauriform *Brachiosaurus* retains a plesiomorphic count of 13 cervical vertebrae, but exhibits great elongation of these elements, whereas *Euhelopus* increases its cervical vertebral count to 17 without significant elongation of individual vertebrae. Although it is clear that *Erketu* had elongate individual vertebrae, poor knowledge of the vertebral counts of basal titanosaurs precludes a phylogenetically informed estimate of the total number of cervical vertebrae.

The morphology of the cervical series reflects accommodation of stresses associated with extreme length. Osteological correlates of the extensor musculature are strongly developed. The long extensor muscle M. ascendens cervicalis originates on the tuburculum ansa and overlaps one or more intermediate vertebrae before inserting on the torus dorsalis in living birds and is hypothesized to have had the same attachment sites in sauropods (Wedel and Sanders, 2002). The hypertrophied prezygodiapophyseal lamina of *Erketu* is most likely associated with the attachment of this muscle as it overlaps vertebrae (fig. 12). The torus dorsalis is likewise powerfully developed in *Erketu*. The tuberculum ansa is rugose and projects posteriorly from the ansa costotransversaria in cervical five, though its development is weaker in cervical four. The development of features associated with M. cervicalis ascendens are weakest in the third cervical, which is not unexpected at the most anterior portion of the neck.

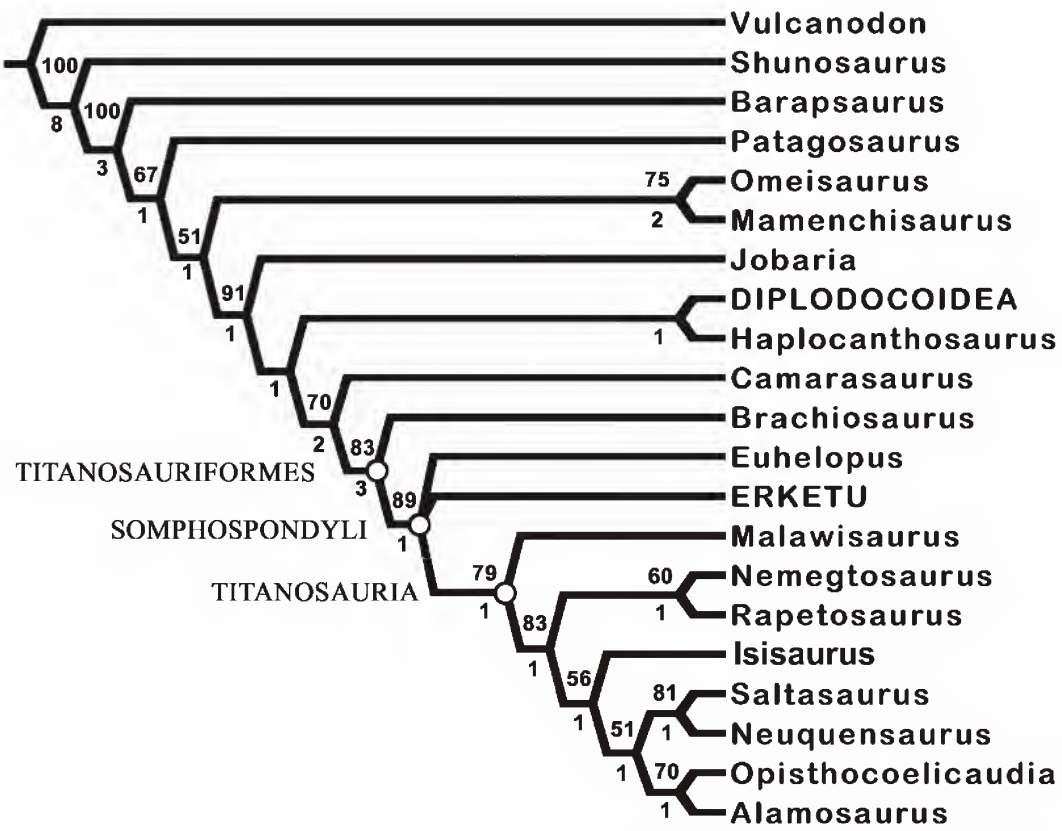

Fig. 11. Strict consensus of six most parsimonious trees of 434 steps derived from analysis using the matrix, character orderings, and coding strategies of Wilson (2002) with the addition of *Erketu*. Bootstrap values were calculated in PAUP*4.0b10 from 1,000 replicates with TBR branch swapping. Bootstrap values >50 are shown above the node they refer to. Decay values calculated manually in PAUP*4.0b10 are shown below the node they refer to.

Tshuihiji (2004) discussed bifurcation of the neural spine in sauropods and the extant ratite *Rhea americana* and concluded that the space between the metapophyses housed extensor ligaments, and possibly epaxial musculature as well. Tshuihiji inferred that the rugose tubercles present posteriorly between the metapophyses of *Apatosaurus* and *Camarasaurus*

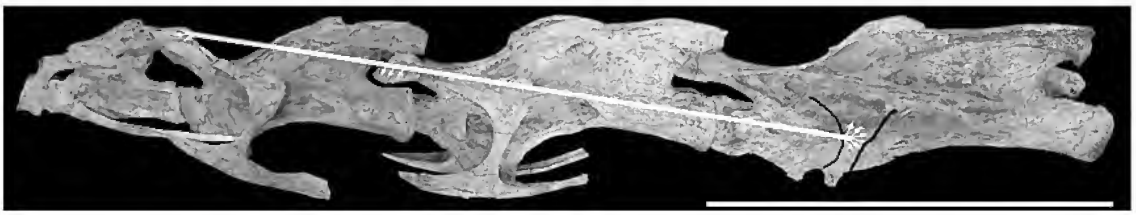

Fig. 12. Artificially articulated anterior cervical series of IGM 100/1803 illustrating the relative length increase between vertebrae. The ansa costo-transversaria is reconstructed on the sixth vertebra. Note that all cervical ribs in this figure are incomplete; preserved ribs overlap at least one succeeding centrum, but have not been reattached due to their fragile nature. The hypothesized position of M. ascendens cervicalis shown in white, with small arrows indicating attachment sites (after Wedel and Sanders, 2002: fig 2). Scale bar = 50 cm.

served as insertion points for a ligament similar to lig. elasticum interspinale in *Rhea*, which would serve to exert a supporting tensional force when the neck was tilted below the level of the ligament's origin at the shoulder region. Tshuihiji noted that the leverage of this force would be increased by lowering the insertion point into the cleft of a bifid neural spine, as opposed to an insertion on the dorsal surface of a single spine. Median tubercles are not present in the known cervicals of *Erketu*. However, the tubercle first arises on cervical ten in *Apatosaurus* (Gilmore, 1936), so this absence may be due to the termination of this ligament system in the middle part of the cervical column.

As elongation of the neck increases, the functional benefits of bifurcation should increase concomitantly. However, the distribution of bifid neural spines in sauropods is not necessarily correlated with neck elongation. Bifurcation is present in both long-necked (*Diplodocus, Barosaurus*) and shorter-necked (Dicraeosaurids, *Apatosaurus*) diplodocoids and independently derived in the short-necked *Camarasaurus*, the long-necked *Mamenchisaurus*, and some titanosauriforms (*Rapetosaurus, Euhelopus*). Furthermore, many sauropods possessing extremely elongate necks, such as brachiosaurids and *Omeisaurus*, lack bifurcation.

Camellate internal structure evolved at least twice in sauropods, and is seen in the long-necked *Mamenchisaurus* and both long- and short-necked titanosauriforms. The relative weight reduction and structural strength of camellate vertebral design versus the camarate design seen in other sauropods is unclear, though initial analysis suggests equal bone reduction can be achieved with either of the two (Wedel, 2004).

The history of Asian sauropods is complex. The Jurassic sauropod fauna belong to a primitive, possibly endemic radiation, whereas the Cretaceous fauna appears to be composed entirely of Titanosauriformes (Wilson, 2005). Whether *Euhelopus* belongs within the Titanosauriformes (Wilson, 2002) or outside Neosauropoda (Upchurch, 1998; Upchurch et al., 2004) remains controversial. Although Titanosauria is one of the most widespread and successful clades of Cretaceous dinosaurs, the interrelationships within this group are incompletely understood. *Erketu* occupies a position of potential importance in understanding the transition from Titanosauriformes to the derived Titanosauria. Continuing work at Bor Guvé and other Gobi localities will help elucidate the history of this group. Notably, cylindrical, unexpanded sauropod teeth are among undescribed material recently collected at Bor Guvé. If these teeth can be confidently assigned to *Erketu*, it would make a strong argument that this taxon can be nested within derived Titanosauria.

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APPENDIX 1

ERKETU ELLISONI MEASUREMENTS (IN MILLIMETERS)

Vertebrae	Centrum length	Centrum height (at cotyle)	Centrum width (at cotyle)
Axis	160	49	50
Cervical 3	268	60	46
Cervical 4	387	70	55
Cervical 5	489	57 (deformed)	85 (deformed)
Hindlimb		Proximodistal length	Distal breadth (anterior face)
Tibia		710	218
Fibula		750	—

APPENDIX 2

CODINGS FOR *ERKETU* FOR CHARACTER MATRIX OF WILSON (2002) USED IN PHYLOGENETIC ANALYSIS

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